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Spatial Characteristics of Cortical Visual Receptive
Fields: Estimation by Metacontrast

by
Ronald Growney

Thesis Submitted to the Faculty of the Graduate School
of Loyola University of Chicago in Partial Fulfillment
of the Requirements for the Degree of
Master of Arts
June, 1970

LIFE

Ronald Growney was born in Chicago, Illinois. He graduated from LaSalle Institute, Glencoe, Missouri in June, 1957. He attended St. Mary's College, Winona, Minnesota and graduated in June, 1961 with a Bachelor of Arts degree. He is presently pursuing a Ph.D. degree in Experimental Psychology at Loyola University.

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CHAPTER I

INTRODUCTION

The general purpose of this study is an investigation of spatial properties of receptive fields in the human visual cortex. The types of receptive fields in Area 17 of the cortex are assumed to be similar in their spatial arrangement of inhibitory and excitatory areas to those found by Hubel and Wiesel (1968) in their study of the monkey cortex. A strategem for the psychophysical study of such fields has been suggested by Weisstein (1969). This strategem is based on her model (Weisstein, 1968) of metacontrast as a lateral inhibition phenomenon. Since certain metacontrast functions are sensitive to the postulated interplay of inhibition and excitation, they may serve as behavioral correlates of neurophysiological single cell recordings. Information about receptive fields may be obtained from characteristics of the masking curve and changes in these characteristics for different stimulus arrangements.

Lyubinskii et al (1968) have shown that if a neuron layer is modeled as a homogeneous, plane layer with lateral connections, the input-output relationship of the layer may be described by the convolution integral

$$F_m(t) = \int_0^t W(t, \tau) F_{m-1}(\tau) d\tau$$

where $F_m(t)$ is the output of the layer and $F_{m-1}(\tau)$ is its input.

$W(t, \tau)$ is the weighting function which models the physical properties of the layer. Hubel and Wiesel (1968) have suggested that the receptive fields of cortical visual cells are formed by excitatory and inhibitory collaterals from prior neural layers. Assuming that each level of this hierarchical organization from transducer to cortical cell can be represented by a homogeneous layer with lateral connections, the cascade of weighting functions may be represented by a composite weighting function, $W_c(t, \tau)$ (see Fig. 1a). The resultant output of the cortical cell, then, can be characterized by an application of $W_c(t, \tau)$ to the stimulus, input excitation front. Since $W_c(t, \tau)$ embodies the physical properties of the cascaded neural layers, $W_c(t, \tau)$ should be similar to the receptive fields of cortical cells, the excitatory center with inhibitory flank cells being chosen as the prime model (Westheimer [1965, 1967] suggested ganglion cell receptive fields as a possible model for his results). As an initial hypothesis, $W_c(t, \tau)$ can be expressed as the sum of two Gaussian functions, one excitatory and one inhibitory, which differ in width and amplitude (see Fig. 1b).

In this context, metacontrast seems well suited as an investigative tool. Suppose the composite weighting function is centered on the edge of the target (movement of $W_c(t, \tau)$ right or left of this point yields decreased excitation) as in Figure 1c and that R_E and θ are small as compared to R_j . If mask width, M , equals R_j , then the masking effect should be at a maximum for simultaneous excitation of the excitatory and inhibitory

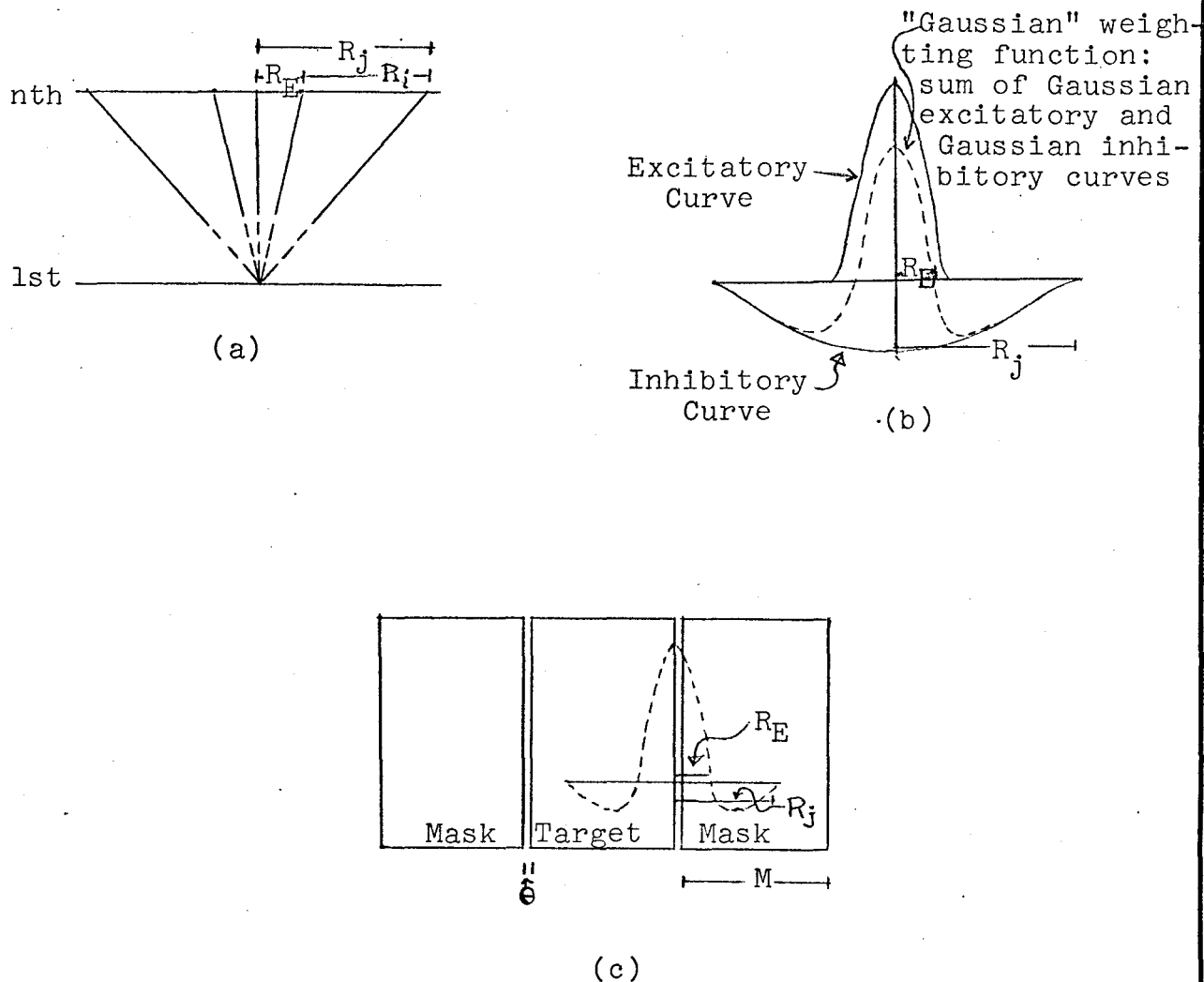


Figure 1 - Comparison of $W_c(t, \tau)$ with a metacontrast paradigm.

- (a) Schematic of $W_c(t, \tau)$ from the stimulus input excitation front to the cortical cells about one point. R_E and R_j represent the spray of excitatory and inhibitory effects from layers 1 to n. R_E and R_I represent the effective regions of inhibition and excitation at layer n.
- (b) $W_c(t, \tau)$ in its continuous representation as summing the excitation and inhibition about any point.
- (c) The application of $W_c(t, \tau)$ to one point on the stimulus input excitation front. The stimulus consists of center target with flanking masks. M is the width of the mask; θ is the angular separation between target and mask.

portions of the receptive field, that is, for $M=R_j$, inhibition will have its greatest effect in diminishing the target excitation. If $M<R_j$, however, the weighting function hypothesis predicts a smaller masking effect due to a smaller covering of the effective inhibitory portion resulting in decreased inhibition. This decrease in masking has been demonstrated for overlapping stimuli by Westheimer (1965). And for $M>R_j$, smaller masking should result due to the disinhibition resulting from the overlap of receptive fields. Disinhibition has been demonstrated experimentally by Frumkes and Sturr (1968) and by Westheimer (1967) who have shown that the larger the mask, the less the masking. Therefore, a comparison of masking effects for masks of different sizes should determine R_j and demonstrate the above effects predicted by the weighting function hypothesis and already found for different experimental conditions.

Receptive field dimensions have been investigated by other techniques. Békésy (1960) has hypothesized that the width of an inhibitory arm of the weighting function, R_j , is equal to one-half the width of a Mach Band (if R_E is small). This yields $R_j \approx R_i = 10'$ to $15'$ in width. Using Beitel's study of the influence of steady-state illumination on the threshold of neighboring areas to a flash of illumination, Taylor estimated $R_j = 10'$ of arc. Both of these figures result from measures made under steady-state conditions and are thought to be retinal effects (Ratliff, 1965). Relevant metacontrast studies are the results of transient excitatory-inhibitory interaction and result in substantially

larger figures for R_j . Fry (1947) found that inhibitory effects of flashes of light in a metacontrast paradigm disappeared at a distance of 75' of visual arc. This value is consistent with other studies in which metacontrast effects were effectively zero by an edge to edge separation of 60' to 120' of visual arc (Alpern, 1953) or by a separation of 85' (Weisstein and Growney, 1969). Assuming a Gaussian distribution of the inhibitory effects and accepting the masking effect as effectively diminished at three standard deviations or $\sim 99\%$ drop in the masking amplitude, metacontrast studies predict $R_j \approx 80'$. This value has been obtained by varying visual angle, θ , between target and mask in the above studies. A more direct method is to vary mask widths and determine the mask size giving maximum masking. This value should correspond to R_j .

It is interesting to contrast these values of R_j with receptive field sizes of cortical visual cells. Hubel and Wiesel (1968) found chiefly two kinds of cells with antagonistic surrounds. Simple cells, predominantly monocular, had receptive fields in the range (length x width) of 15' x 15' up to 30' x 45' while the lower hypercomplex cells, predominantly binocular, had receptive fields 1 1/2 to 2 times as big: that is, a range of 22.5' x 22.5' up to 60' x 90'. Assuming a uniform distribution of cells over these ranges, the average simple cell R_j is 15' in width; the average lower hypercomplex R_j is 33'. This suggests that the metacontrast phenomenon, if it takes place at the visual cortex, is not a property of single summary cells where $R_j = 33'$,

but of the output wavefront of the relevant neural layer with $R_j \approx 80'$. This means that cells in the visual cortex function not only as unit property analyzers but also as points on a higher-level wavefront. It may even be possible to infer the general level of this wavefront if monoptic and dichoptic metacontrast paradigms yield different estimates of R_j . Generally, monoptic and dichoptic masking functions have been found to differ in shape (Schiller and Smith, 1968; Weisstein and Grownay, 1969). Both may be central effects; Schiller (1968), for example, found no metacontrast effects in the cat L.G.B. Then, if a monoptic masking paradigm yields smaller values for R_j than does the dichoptic paradigm, this may suggest that the monoptic masking effect occurs in a neural layer composed chiefly of monocularly driven cells, as the simple cortical cells, and that the dichoptic masking effect is associated with a wavefront from a neural layer composed of binocularly driven cells as the lower hypercomplex cells. These specific layers would not be pointed out by different estimates of R_j but differing neural layers with different eye dominance characteristics would seem to be indicated.

R_E , the excitatory radius of the composite weighting function, is more difficult to measure. Westheimer (1967) found a decrease in masking for masks smaller than $5'$ in diameter. His overlapping stimuli were presented foveally using a target $1'$ in diameter. This diminishing of the masking effect can be expected as R_j approaches zero and is predicted by the weighting

function hypothesis. A comparison of the weighting function to a slice through the diameter of this circular stimulus arrangement shows that R_j is certainly greater than 2.5' in width and that R_E is certainly smaller than 2.5' in width. Masks of different sizes in a metacontrast paradigm could also determine a size maxima for R_E . As can be seen in Figure 1c, a mask sufficiently small and sufficiently close to the target would not be inhibitory at all but fall within R_E . This facilitatory effect should be found for a very small mask close to the target.

One of the assumptions of the weighting function hypothesis is the regular distribution of excitatory and inhibitory fibers within the neural layer being studied. This assumption can be tested by using targets of varying widths. If R_j is consistent for targets of different widths, this would indicate that the distribution of fibers does not change abruptly, at least and that the weighting function determined by R_j is valid over that region covered by the targets. From neurophysiology it can be expected that the distribution of fibers (and hence, R_j) changes for targets presented to different parts of the retina. Indeed, Westheimer (1965, 1967) found significant differences in threshold effects for foveal and peripheral stimuli. Over a limited region, however, the weighting function predicts no difference for different sized targets. To the extent there is a difference, the weighting function does not hold uniformly. In fact, the target might be involved in determining the size of the resultant wavefront receptive field. In that case, the weighting function

hypothesis would not hold simply.

In this experiment, then, different sized masks and targets will be used to investigate cortical receptive fields which may not be the same thing as cortical cell receptive fields. Specific hypotheses are: (1) Masking amplitudes for different sized masks should follow the curve of Figure 2. This means masking should be at a maximum for $M \approx 80'$. Masking should decrease for $M < 80'$ and fall to zero for some $M > 0$. Facilitation may be found for masks sufficiently small. For $M > 80'$ masking should diminish due to disinhibition. (2) There should be no difference in estimates of R_j for different sized target. (3) Compare monoptic and dichoptic data for differences in R_j .

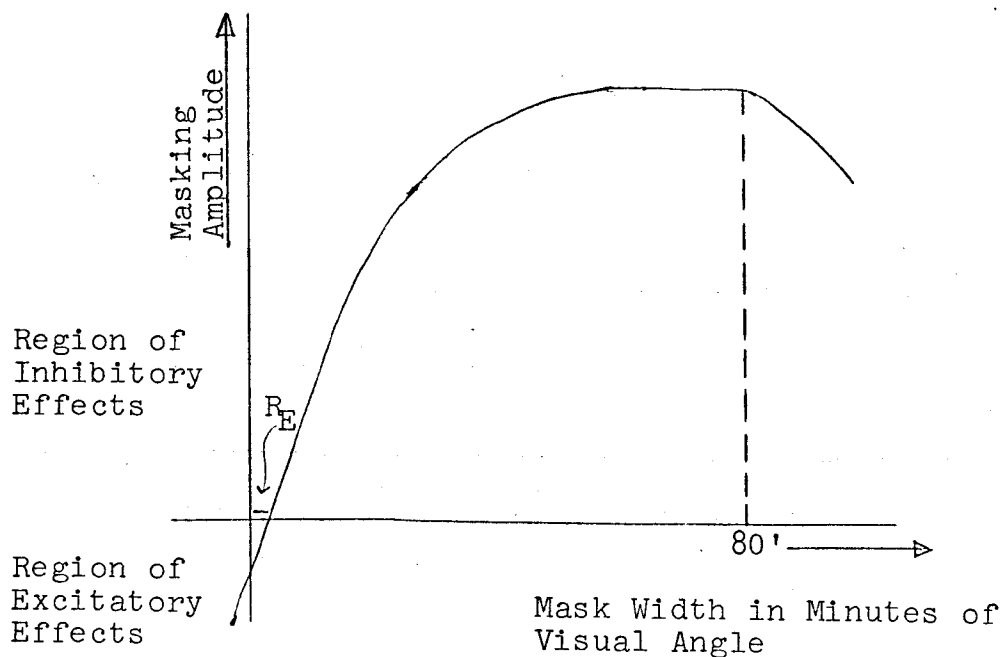


Figure 2 - Predicted masking amplitudes for masks of different widths.

CHAPTER II

METHOD

Three students with 20/20 corrected vision were paid to serve as subjects.

The display was presented on a six-channel binocular tachistoscope (Scientific Prototype Manufacturing Corporation, Type G). The stimuli were illuminated rectangles against a constantly illuminated 8ft-L background. Stimulus luminance was 16ft-L, measuring the blank stimulus field. Illuminance measurements were made with an SEI Photometer and monitored by photo-cells placed in each channel with the output displayed on a Tektronix Oscilloscope, Model 504. Illumination was varied by means of intensity controls on the tachistoscope and by neutral density filters.

The stimuli were slide negatives on Kodak Ortho-Type III film. All stimuli were of one height, 0.141 inches subtending a visual angle of 49.5 minutes with the 1.65 channel lens. Four target sizes were used with widths in visual angle of 1', 8.4', 24.6', and 49.2'. There were four sets of masks, each set corresponding to one target size. Each mask consisted of two equal sized rectangles flanking the target on each side with a target-mask separation of $\theta = 45^\circ$ of visual angle. Each set of masks consisted of eleven rectangle sizes with widths in visual angle of $M = 1', 2.8', 4.2', 8.4', 12.2', 16.1', 24.6', 33.6', 49.2', 73.8', \text{ and } 98.4'$. Each target and mask was exposed

individually for a duration of 16 msec. Each stimulus presentation was separated by a 5 second interval.

A fixation X crossing the entire visual field was used to facilitate the aligning of the dichoptic field and the center of the X served as fixation point. The stimulus display was centered 1° below and 1° to the right of the fixation point. S adapted to the background luminance for 10 minutes prior to each day's session.

The Steven's magnitude estimation procedure was used with a modulus of 10 assigned to the luminance of the target flash presented by itself. This standard was shown to S at the beginning of each trial. At the beginning of the experiment, each S was run through 10 practice hours in which each target with its equal sized mask was presented for 15 trials. Only targets 3 and 4 (24.6' and 49.2' in width respectively) appeared under both monoptic and dichoptic conditions. Targets 1 and 2 (1' and 8.4') were presented monoptically only. Each target was practiced monoptically for 1 session. Targets 3 and 4 were practiced dichoptically for 3 sessions each. Each practice trial consisted of 16 ISI's over a range of -40 to 240 msec.

For the experiment itself, each target-mask-ISI combination was shown in both monoptic and dichoptic states (exceptions noted above) and each target-mask-ISI-state element was replicated 10 times. One trial consisted of 17 ISI over the range -100 to 200 msec in 20 msec steps (omitting ISI=180 msec), each set presented in randomized order. Each experimental session

consisted of 22 trials. The session consisted of 1 state and 1 replication at each ISI for all target-mask combinations for 2 targets. The states were randomized from session to session. A random order for the 4 targets was selected. Then for each session 2 targets were presented with their randomized set of 11 masks, so that target 1 with its 11 masks was run, constituting the first 11 trials, then target 2 with its 11 masks.

Each subject attended a total of 40 experimental sessions: 10 practice hours and 30 sessions, each session 80 minutes in length and consisting of 374 responses per session.

CHAPTER III

RESULTS

Since magnitude estimations tend to give log normal distributions (Stevens, 1966), two analyses of variance were performed on the logarithmic transformation of the data. Two analyses were necessary since not all targets were run under dichoptic conditions, only targets T3 and T4. The analysis of variance model used was the mixed model with r subjects measured m times under fixed conditions. The error term for this model is the interaction including subjects, which is the next order term from the term in the numerator. The difficulty of the task in giving brightness estimations for T1 and the variability of the results for T1 resulted in dropping T1 from the study. In the figures that follow, the peak masking amplitude for subject 1 was at ISI=20. For subjects 2 and 3, peak masking was consistently at ISI=40.

A four-way analysis of variance was performed on the monoptic data for T2, T3, and T4. The significant effects ($p < .01$) are summarized in Table 1. Masks differed significantly across conditions, a difference attributable chiefly to the drop in masking amplitude for small masks. This drop can be most clearly seen in Figures 3 and 5. It is also apparent in Figure 4 where masks of selected sizes are graphed across ISI. That the observed differences are significant is shown by interaction 34. Interaction 23 and 24 show that different size

TABLE 1

4-Way Analysis of Variance: Significant Effects

Main	1st Order	2nd Order
3	23	234
4	24	
	34	

1. Subjects. 2. Targets (T2, T3 and T4). 3. Masks
4. ISI ($p < .01$).

targets were differentially effected by different masks or different ISI's. The reason for the significance of these interactions and the second order, 234, interaction seems to be the difference within the data of subject 1 comparing T2 with T3 and T4 combined. This is shown in Figure 3. It can also be seen that the data for subjects 2 and 3 show little or no difference between targets. The significance of the main effect for ISI is expected in this metacontrast paradigm and is reflected in the U-shaped masking functions for different size masks shown in Figure 4.

A five-way analysis of variance was performed on the complete data for T3 and T4. The significant effects ($p < .01$) are summarized in Table 2. The chief variable of interest here is state (2), the distinction between monoptic and dichoptic presentations. The data of subject 1 again shows quite a bit of variability in Figure 5 whereas the data of subjects 2 and 3 show a high similarity for monoptic and dichoptic estimations. Differences between states for different masks or different

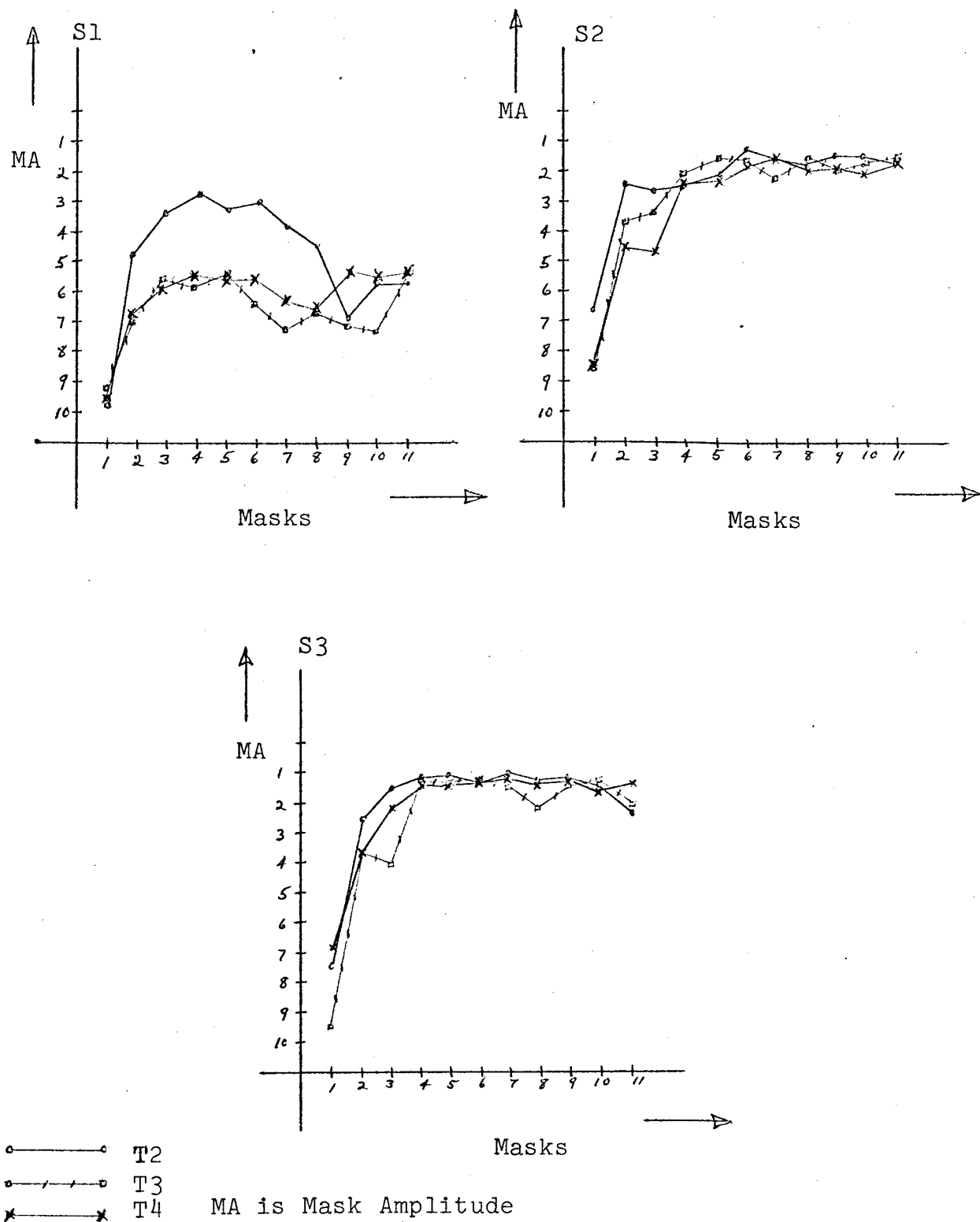
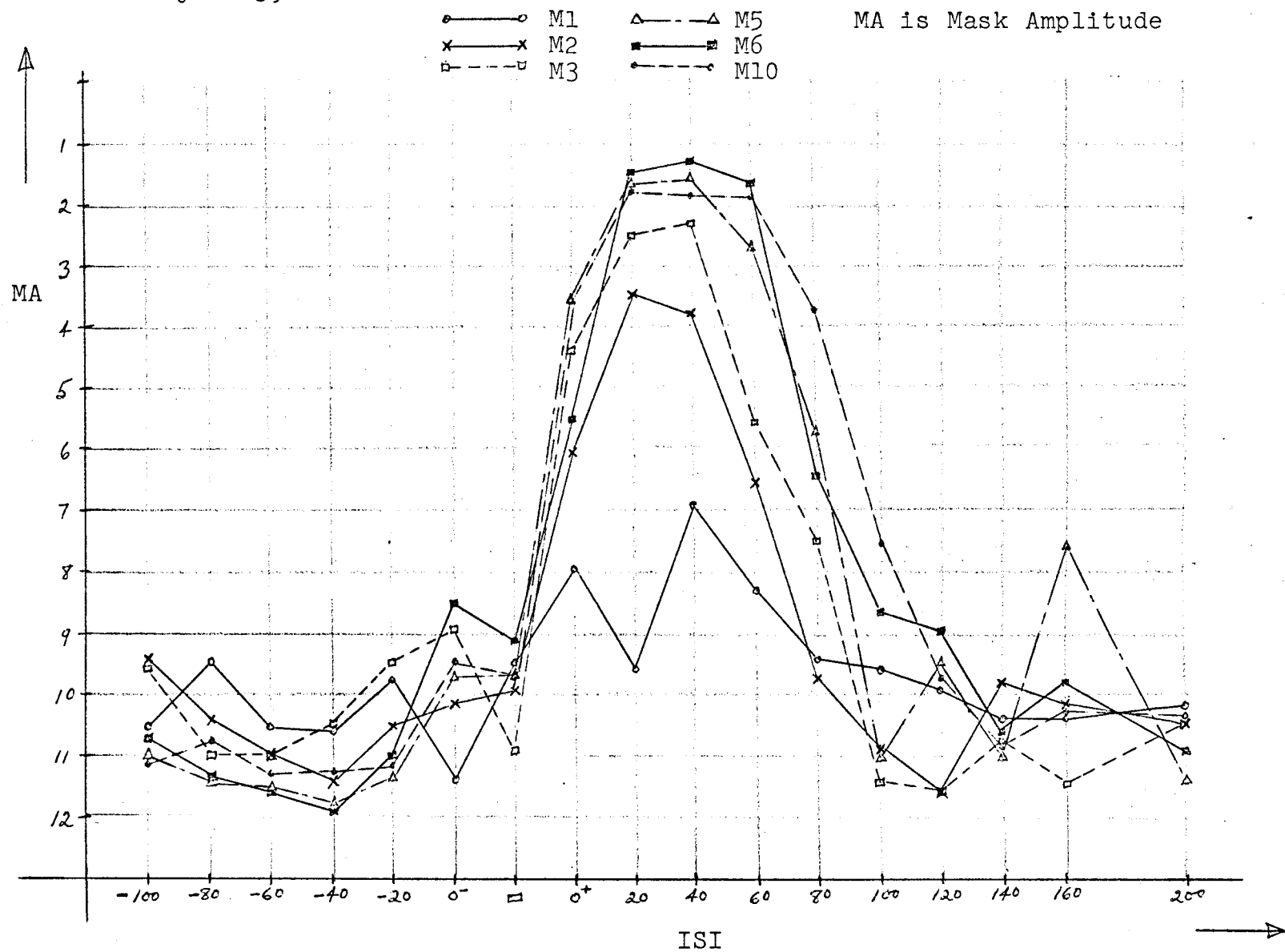


Figure 3 - Peak masking amplitude for each mask for T2, T3 and T4 for each subject (S1, S2 and S3). Monoptic Data.

Figure 4 - Masking function for selected masks at each ISI for the monoptic data of subject 3, T4.



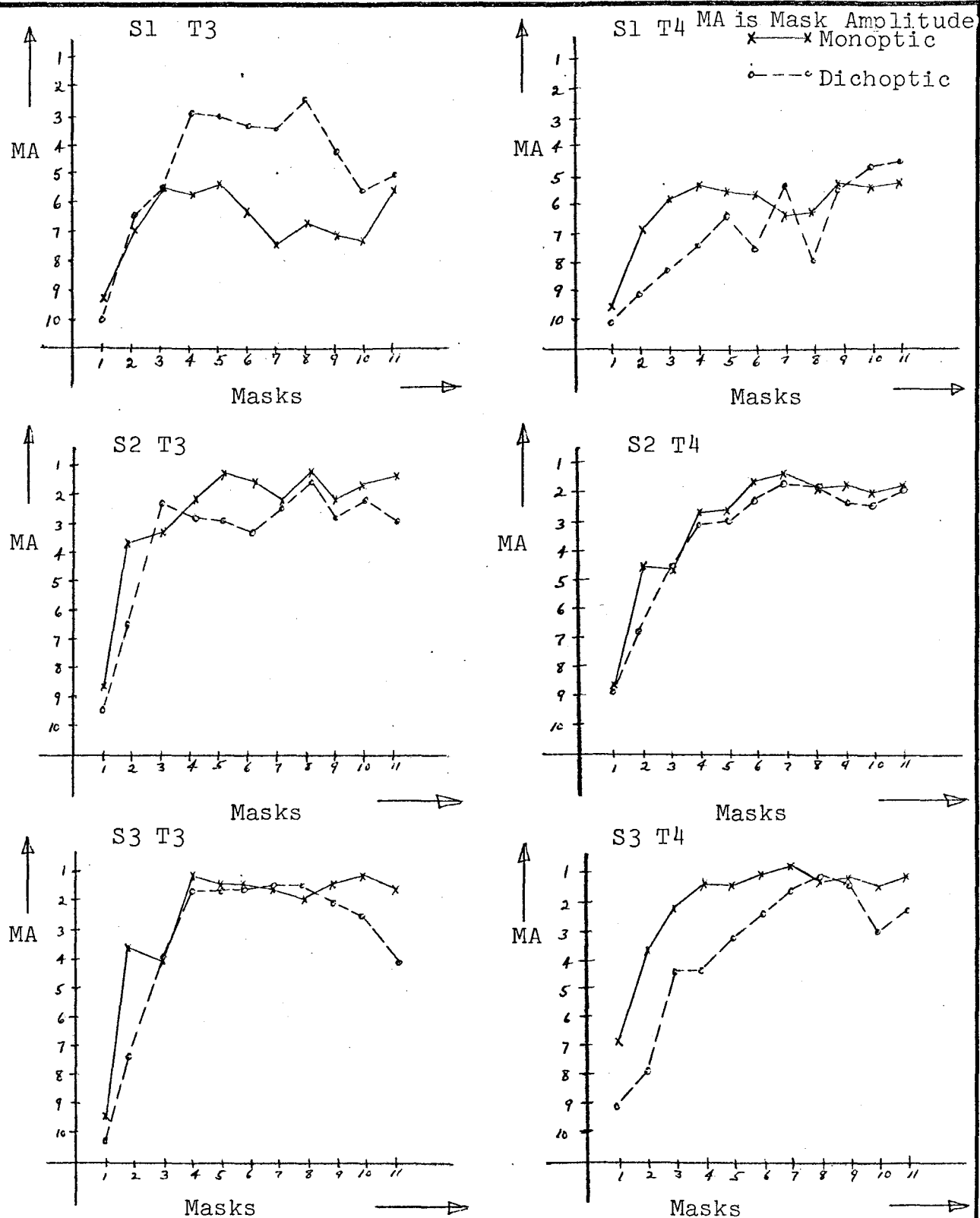


Figure 5 - Peak masking amplitude for each mask, comparing monoptic and dichoptic data for each subject on T3 and T4.

TABLE 2

5-Way Analysis of Variance: Significant Effects

Main	1st Order	2nd Order
4	24	234
	25	235
	34	245
	45	

1. Subjects. 2. State (Monoptic or Dichoptic).
 3. Targets (T3, T4). 4. Masks. 5. ISI ($p < .01$).

ISI's are significant, however, as shown by the significance of interactions 24 and 25. The interaction between state and mask seems due partly to the differences in the data of subject 1 but also to a tendency for smaller masking peaks for dichoptic data contrasted with monoptic data for the smaller masks. The significant difference between masks (main effect 4, shown in Figure 5) and the significant interaction between masks and ISI (interaction 45) show that the decrease in masking amplitude for small masks holds across subjects, targets and states.

CHAPTER IV

DISCUSSION

A comparison of Figures 3 and 5 with Figure 2 shows that the observed masking amplitudes followed, in general, the predicted curve. Essential to support of the weighting function hypothesis is the diminished amplitude of the masking function for small masks; masking should diminish as the hypothesized inhibition is diminished by smaller mask size. This smooth and consistent drop in amplitude is clearly shown in Figures 3, 4 and 5. This sharp drop means that most of the effective inhibition in the inhibitory Gaussian curve is concentrated within a radius of $10'$. It is interesting that this estimate of $10'$ is similar to Bekesy's and Taylor's estimate of $R_j=10'$. In Bekesy's estimation of Mach Bands, for example, the phenomena may be chiefly retinal in origin. On the other hand, since it is something perceived, it is also possible that it is a composite result of the application of $W_c(t, \tau)$. $R_j=10'$, then, may be a measure of effective inhibition of $W_c(t, \tau)$ and not a measure of the first stage, retinal weighting function. Except for the weighting function hypothesis, it might not be expected that R_j should be greater than its effective region. It's the weighting function hypothesis which predicts R_j can only be measured in relation to where disinhibition sets in.

There was no obvious drop in amplitude as expected, however, after $M_{10}=74'$. While some individual curves show a drop

for $M_{11}=99'$ as compared to M_{10} , just as many do not; so disinhibition was not demonstrated. This means that R_j cannot be specified by these data. Masking remained at a relatively constant peak over the range of masks $10'$ to $100'$ in width for targets $10'$ to $50'$ in width presented foveally. This $100'$ upper limit is within the $60'$ to $120'$ range within which Alpern (1953) noted masking amplitude dropped to zero. Since disinhibition has been found by others (Westheimer, 1967; Frumkes and Sturr, 1968), it is quite possible that a drop in masking amplitude would have been observed for slightly larger masks, as masks $110'$ and $120'$ in width. However, these data do support a lower limit on R_j of $R_j \geq 80'$.

Since masking and not a brightening of the target occurred for M_1 (see Figures 3 and 5), R_E is smaller than the sum of $\theta=45''$ plus $M_1=1'$, that is, $R_E \leq 2'$ as an upper limit, according to the weighting function hypothesis. This figure is consistent with the upper limit set by Westheimer's (1967) data of $R_E \leq 2.5'$ and narrows it somewhat further. This conclusion is valid insofar as the edges are important in perceiving the target and the edges are sufficiently narrow.

The main effect of targets was not significant. However, there is striking difference in the monoptic data of subject 1 between targets, a difference not reflected in the data of the other subjects. Part of the difficulty in comparing targets, though, may have been the relative standards employed, as presenting T_2 alone as a standard for brightness estimations of T_2 ,

T3 alone as a standard for brightness estimations of T3, and similarly for T4. In future studies, a single standard should be employed for all brightness estimations, thus insuring the comparability of the targets.

Monoptic and dichoptic data cannot be compared as to differences in R_j since R_j could not be specified. A surprising result, however, is that both subjects 2 and 3 show similar peak amplitudes for monoptic and dichoptic data (see Figure 6). The data of subject 1 for T3 (Figure 6) is closer to what has been previously reported (Schiller and Smith, 1968; Weisstein and Growney, 1969). Dichoptic data is usually higher in amplitude than monoptic data besides the differences in shape. This difference in amplitude was not observed for subjects 2 and 3, though there was some tendency for dichoptic data to be even smaller in amplitude than monoptic data for small masks, $M < 5'$ (see Figure 6). It is not surprising then, that the main effect of state was not significant.

In summary, the weighting function hypothesis is partially supported by the shape of the masking amplitude vs mask width experimental curve. An upper limit of $R_E \leq 2'$ of visual angle is predicted by use of the weighting function hypothesis as is a lower limit on R_j of $R_j \geq 80'$ of visual angle. However, R_j could not be specified due to lack of disinhibition at $M_{ll} = 99'$. While R_E is probably very narrow, $R_E \leq 2'$, the shape of the inhibitory Gaussian curve must also be rather narrow with most of the effective inhibition within a radius of $10'$. This suggests that

some different estimates of R_j may be due to measuring only part of R_j ; a metacontrast design with a suitable number of mask sizes should be adequate in view of the weighting function hypothesis and previous experimental findings. A future investigation of this topic should be able to specify R_j by (1) including several mask sizes greater than $M=100'$; (2) using a single standard for all brightness estimations such as a circle of intermediate radius; and (3) using the convergent operation of varying θ , the angular separation between target and mask, for masks of different widths. The weighting function hypothesis has important applications as a theoretical tool and should be explored fully.

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APPROVAL SHEET

The Thesis submitted by Ronald Growney has been read and approved by members of the Department of Psychology.

The final copies have been examined by the director of the Thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the Thesis is now given final approval with reference to content and form.

The Thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Arts.

June 2, 1970
Date

Naom Weiss
Signature of Advisor